Biological Report 82(11.73)
August 1987

TR EL-82-4

Species Profiles: Life Histories and Environmental Requirements of Coastal Fishes and Invertebrates (South Florida)

REEF-BUILDING CORALS

Fish and Wildlife Service

U.S. Department of the Interior

Coastal Ecology Group
Waterways Experiment Station

U.S. Army Corps of Engineers

Bio. Rept. **82(11.73)** Species Profile: (South Florida) Reef-Building Corals

Erratum

P2. left column, paragraph 4, sentence 3 should read:

Both species of Montastraea, but no species of Acropora, occur on the Texas Flower Garden Banks (Bright and Pequegnat 1974; Bright et al. 1984), and in Bermuda (Laborel, 1966; Sterrer 1986). Neither Acropora nor Montastraea occurs on the Florida Middle Grounds (Hopkins et al. 1977).

Hopkins, T..S., D. R. Blizzard, S. A. Brawley, S. A. Earle, D. E. Grimm, D. K. Gilbert, P. G. Johnson, E. H. Livingston, C. H. Lutz, J. K. Shaw, and B. B. Shaw. 1977. A preliminary characterization of the biotic components of composite strip transects on the Florida Middlegrounds, Northeastern Gulf of Mexico. Proc. Third International Coral Reef Symp. (Miami, FL) 1:31-37.

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Species Profiles: Life Histories and Environmental Requirements of Coastal Fishes and Invertebrates (South Florida)

REEF-BUILDING CORALS

by

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Performed for

Coastal Ecology Group
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National Wetlands Research Center
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PREFACE

This species profile is one of a series on coastal aquatic organisms, principally fish, of sport, commercial, or ecological importance. The profiles are designed to provide coastal managers, engineers, and biologists with a brief comprehensive sketch of the biological characteristics and environmental requirements of the species and to describe how populations of the species may be expected to react to environmental changes caused by coastal development. Each profile has sections on taxonomy, life history, ecological role, environmental requirements, and economic importance, if applicable. A three-ring binder is used for this series so that new profiles can be added as they are prepared. This project is jointly planned and financed by the U.S. Army Corps of Engineers and the U.S. Fish and Wildlife Service.

Suggestions or questions regarding this report should be directed to one of the following addresses.

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or

U.S. Army Engineer Waterways Experiment Station
Attention: WESER-C
Post Office Box 631
Vicksburg, MS 39180

W

CONVERSION TABLE

Metric to U.S. Customary

Multiply	By	To Obtain
millimeters (mm)	0.03937	inches
centimeters (cm)	0.3937	inches
meters (m)	3.281	feet
meters (m)	0.5468	fathoms
kilometers (km)	0.6214	statute miles
kilometers (km)	0.5396	nautical miles
square meters (m^2)	10.76	square feet
square kilometers (km^2)	0.3861	square miles
hectares (ha)	2.471	acres
liters (1)	0.2642	gallons
cubic meters (m^3)	35.31	cubic feet
cubic meters (m^3)	0.0008110	acre-feet
milligrams (mg)	0.00003527	ounces
grams (g)	0.03527	ounces
kilograms (kg)	2.205	pounds
metric tons (t)	2,205.0	pounds
metric tons (t)	1.102	short tons
kilocalories (kcal)	3.968	British thermal units
Celsius degrees (°C)	1.8(°C) + 32	Fahrenheit degrees
micro Einsteins per square meter per second ($\mu E\ m^{-2}s^{-1}$)	6.02×10^{17}	photons $m^{-2}s^{-1}$
micro Einsteins per square meter per second ($\mu E\ m^{-2}s^{-1}$)	4.67	foot candles
micro Einsteins per square meter per second (μE m-'s-l)	51.22	lux

U.S. Customary to Metric

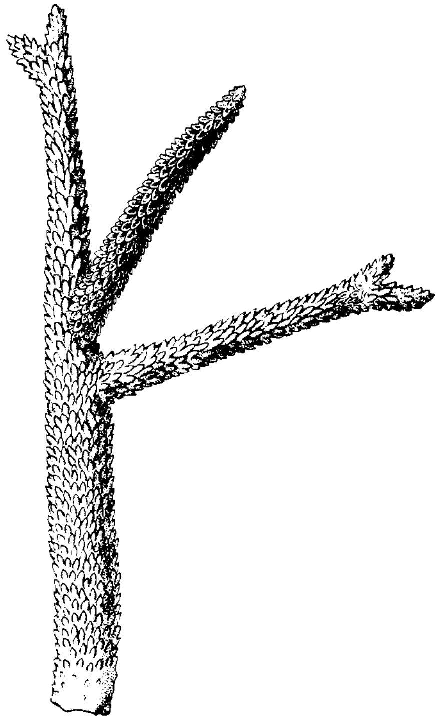
Multiply	By	To Obtain
inches	25.40	millimeters
inches	2.54	centimeters
feet (ft)	0.3048	meters
fathoms	1.829	meters
statute miles (mi)	1.609	kilometers
nautical miles (nmi)	1.852	kilometers
square feet (ft^2)	0.0929	square meters
square miles (mi^2)	2.590	square kilometers
acres	0.4047	hectares
gallons (gal)	3.785	liters
cubic feet (ft^3)	0.02831	cubic meters
acre-feet	1,233.0	cubic meters
ounces (oz)	28,350.	milligrams
ounces (oz)	28.35	grams
pounds (lb)	0.4536	kilograms
pounds (lb)	0.00045	metric tons
short tons (ton)	0.9072	metric tons
British thermal units (Btu)	0.2520	kilocalories
Fahrenheit degrees (°F)	0.5556 (°F - 32)	Celsius degrees
photons $m^{-2}s^{-1}$	1.661×10^{-18}	micro Einsteins per square meter per second
foot candles (fc)	0.21413	micro tinsteins per square meter per second
lux (lx)	0.01952	micro Einsteins per square meter per second

CONTENTS

ACKNOWLEDGMENTS

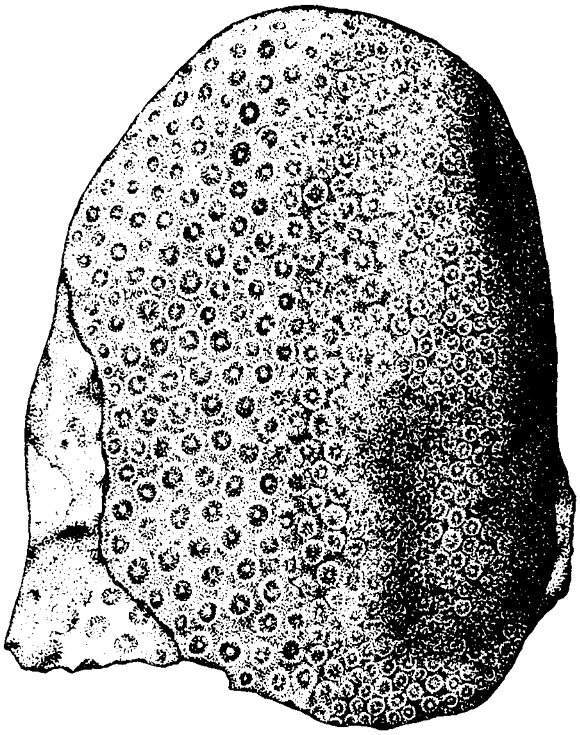
I thank Alex Heller for drawing Figures la - d, and Lawrence Castanares for discussions on the systematics of these coral species. Reviews were provided by Dr. Judith C. Lang, University of Texas, Austin, and Dr. Alina Szmant-Froelich, University of Miami, Florida. This report is Contribution No. 303 from the Discovery Bay Marine Laboratory, Discovery Bay, Jamaica.

4 Elkhorn coral
Acropora palmata

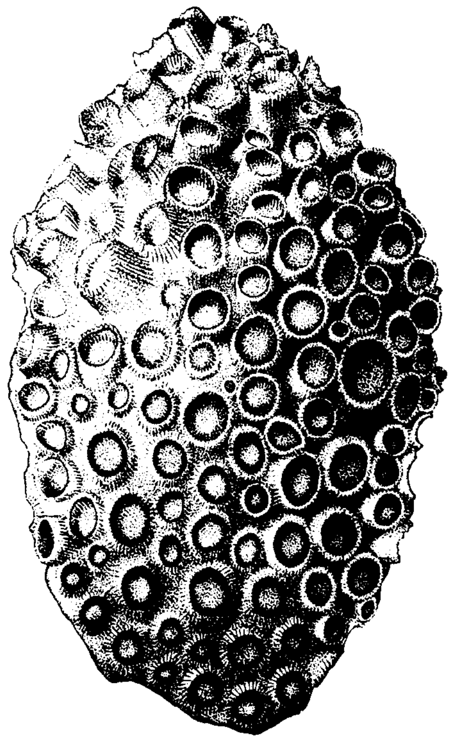


B Staghorn coral
Acropora cervicornis

Figure 1. Major reef-building corals in the Caribbean. (A) Specimen UGA 512; 2 m depth; San Blas, Atlantic Panama. Cnidaria Collection, Museum of Natural History, University of Georgia. (B) Specimen UGA 292; 4 m depth; Jan-Thiel Curacao. Cnidaria Collection, Museum of Natural History, University of Georgia:



C Common star coral
Montastraea annularis



D Large star coral
Montastraea cavernosa

(C) Specimen UGA 379; 2 m depth; Discovery Bay, Jamaica. Cnidaria Collection, Museum of Natural History, University of Georgia. (D) Specimen UGA 1154; 15 m depth; Discovery Bay, Jamaica. Cnidaria Collection, Museum of Natural History, University of Georgia. Drawings by Alex Heller.

REEF-BUILDING CORALS

Information is presented on four major Caribbean reef-building corals, mentioned individually where relevant data exist. The species are compared and contrasted to highlight their similarities and differences.

NOMENCLATURE, TAXONOMY, AND GEOGRAPHIC RANGE

1. Specific name...Acropora palmata (Lamark)

Preferred common name...Elkhorn coral (Figure 1a)

Class........................Anthozoa
Order....................Scleractinia
Suborder.................Astrocoeniia
Family...................Acroporidae

2. Specific name...Acropora cervicornis (Lamark)

Preferred common name...Staghorn coral (Figure 1b)

Class........................Anthozoa
Order....................Scleractinia

Suborder ....Astrocoenii a
Family ....Acroporida e

3. Specific name Montastraea annularis (Ellis and Solander)
Preferred common name ... Common star coral (Figure 1c)
Class ....Anthozoa
Order ....Scleractinia
Suborder ....Faviina
Family ....Faviidae

4. Specific name..Montastraea cavernosa (Linnaeus)
Preferred common name . . . .Large star coral (Figure 1d)
Class ....Anthozoa
Order ....Scleractinia
Suborder ....Faviina
Family ....Faviidae

All four of these corals are found throughout shallow coastal waters of the Caribbean and the western tropical Atlantic (Smith 1948). Montastraea cavernosa is also found in Brazil (Laborel 1967) and the eastern tropical Atlantic (Laborel 1974). All four species are common in southern Florida (L. Agassiz 1852, 1869, 1880; A. Agassiz 1888; Vaughan 1911; Shinn 1963; Ginsburg and Shinn 1964; Kissling 1965; Marszalek et al. 1977; Davis 1982; Halas 1985). Both species of Montastraea, but no species of Acropora, occur in the Florida Middle Grounds, the Texas Flower Garden Banks (Bright and Pequegnat 1974; Bright et al. 1984), and in Bermuda (Laborel 1966; Sterrer 1986).

Goldbera (1973) reported that isolated colonies of Acropora cervicornis, Montastraea annularis, and M. cavernosa occur in deep water (16-30 m) as far north as Palm Beach, Florida. at latitude 26°3' N (Figure 2). Acropora palmata appears first at Fowey Rocks, Florida (lat. 25°37' N), which is also the location of the first major appearance of all of the species in shallow water (Burns 1985). Reef development by these species begins slightly farther south, in Biscayne National Park, Florida, at 25°25' N latitude. Fully developed Acropora palmata and A. cervicornis reef zones are found in Key Largo National Marine Sanctuary at Carysfort Reef, Florida (lat. 25°20' N), and south of there (Jaap 1984; White and Porter 1985). Little is known about coral distribution in the turbid waters off the west coast of Florida (Figure 2).

Contrasting depth ranges and zones of maximum development for these species in Jamaica (Goreau and Wells 1967) are shown in Table 1.

MORPHOLOGY AND IDENTIFICATION AIDS

Both species of Acropora are branching (Figures 1a and b), whereas both species of Montastraea are mound shaped (Figures 1c and d). The blades are flattened and palm shaped in A. palmata (rounder), but narrow and cylindrical in A. cervicornis. Branches emerge at acute angles and generally in the same plane of growth as the parent blade in A. palmata, whereas each blade emerges more at right angles, and generally in a different plane of growth from most of the other blades, in A. cervicornis. Blades of A. palmata are greater than 0.5 m in length, whereas unbifurcated blades of A. cervicornis rarely are. Coloration is highly variable in A. palmata, ranging from very light tan to brown, whereas it is brownish yellow and more uniform in colonies of A. cervicornis. Polyps (the individual units of live coral that make up a colony) of both A. palmata and A. cervicornis are about 0.1 cm in diameter. Acropora cervicornis has a single apical polyp in the growth axis.

Polyps of Montastraea annularis average 0.3 cm in diameter (medium-sized among coral polyps); those of M. cavernosa average 1.0 cm (large for Caribbean corals). In both species, polyp diameter increases and polyp density decreases with increasing

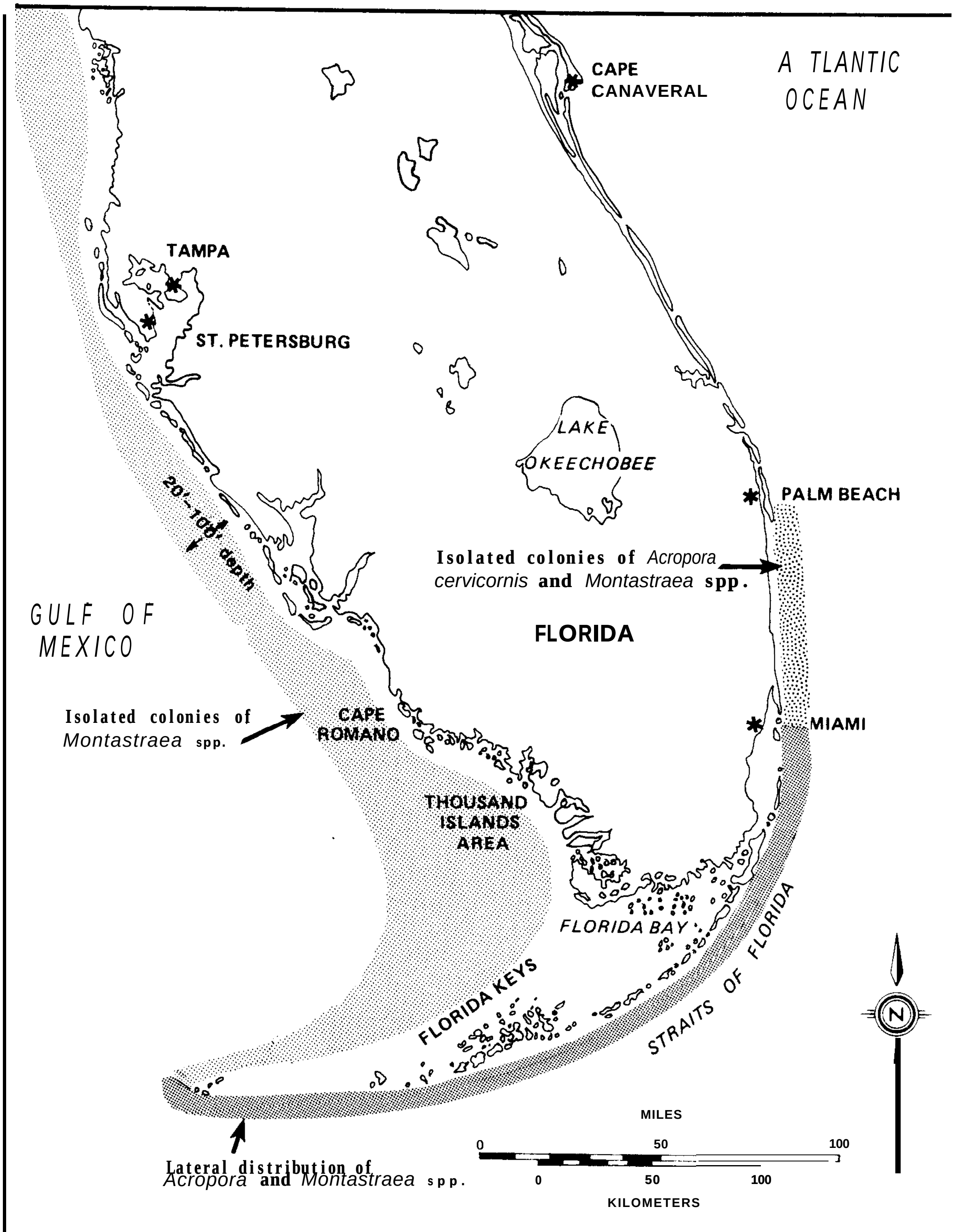


Figure 2. Coastal distribution of the elkhorn, staghorn, common star, and large star corals. Montastraea exists in water depths below 1 m and out to the 40-m contour; Acropora exists on reefs from the surface to 20 m depth.

Table 1. Patterns of depth distribution, abundance, and ecology of Montastraea annularis, M. cavernosa, Acropora palmata, and A. cervicornis.

Species	Depth (m)[a] Range	optimum	Extension[b] rate (cm/yr)	Sex[c]	Spawning[c] season	Spat[c] (No./m^2)	Resistance to hurricane
Acropora palmata	0-15	0-7	5.00-9.50	H	Aug	0.03	M
Acropora cervicornis	0-30	3-20	10.00-26.40	H	Aug	0.01-0.30	L
Montastraea annularis	0-80	3-40	0.68-2.40	H	Aug-Sept	0.45-1.04	H
Montastraea cavernosa	0-90	10-40	0.35-0.57	D	Sept	0.14-1.09	H

[a]Data adapted from Goreau and Wells (1967).
[b]See GROWTH CHARACTERISTICS section of the text for references.
[c]Data adapted from Szmant-Froelich (1985, 1986).
[d]L = low, M = medium, and H = high.

depth (Dustan 1975, 1979; Porter et al. 1987). Although colonies of both species are mound shaped, those of M. annularis that exceed 0.5 m in diameter tend to break into distinct lobes in shallow water; no such tendency exists in large colonies of M. cavernosa. Colonies of M. annularis have a great diversity of shapes in shallow water. Colonies of M. annularis sometimes become 4-5 m in diameter, but those of M. cavernosa rarely exceed 1 m. As water depth increases, colonies of both Montastraea species flatten and become platelike (Dustan 1975, 1979; Graus and Macintyre 1976). At depths of 30-40 m in Jamaica, most colonies of M. annularis grow as flattened rosettes of overlapping colonies. Colonies of M. cavern&a do not flatten completely at depths less than 60 m.

REASON FOR INCLUSION IN THE SERIES

Coral reefs, which are highly attractive to tourists, are the most diverse marine community on earth. Their existence depends on the successful growth and maintenance of a complex, three-dimensional structure in shallow water. This topographically complex form is built primarily by hermatypic corals (those corals bearing symbiotic zooxanthellae). The four species reviewed here are among the primary corals involved in this building process (Lighty et al. 1982).

As stated by Jaap (1984), in southern Florida "the two stony corals most responsible for reef building are Acropora palmata (elkhorn coral) and Montastraea annularis (star coral)."

LIFE HISTORY

Spawning

The four species reviewed here spawn annually in the fall. They all discharge their gametes into the water column, rather than brooding their larvae (Szmant-Froelich 1986).

Montastraea annularis is a simultaneous hermaphrodite (eggs and sperm are present in the same individual at the same time). In Puerto Rico, oogenesis begins in mid-May, and spermatogenesis begins during mid-July (Szmant-Froelich 1985). The annual spawning period is short, occurring immediately after the full moon in late August or September. Colonies larger than 51 cm^2 (estimated age, 4-5 years) are reproductive; smaller colonies, or pieces of colonies below this size, are not (Szmant-Froelich 1985).

Montastraea cavernosa is dioecious. The gametogenic period is similar to that described above for M. annularis. Spawning also occurs annually in late August or September (Szmant-Froelich 1986). Neither minimum colony size nor age at first reproduction is known.

Acropora palmata and A. cervicornis do not differ substantially in reproductive biology. Like Montastraea annularis, they are simultaneous hermaphrodites in which the development period is longer for eggs than for sperm. They differ from M. annularis in having a longer period of egg development of 10 months. As in both species of Montastraea, there is a short spawning season in August. In Puerto Rican populations of Acropora, spawning is synchronous and occurs 6 days after the full moon in August (Szmant-Froelich 1986). The relation between fragmentation and reproduction has not been examined.

Fecundity

Annual egg production per square centimeter of coral tissue is 720 to 2,016 in Montastraea annularis and 288 to 576 in M. cavernosa (Szmant-Froelich 1986). Because eggs of M. annularis are slightly smaller than those of M. cavernosa (300 and 350 pm, respectively), the annual egg mass produced per unit area of living coral tissue by M. cavernosa is double that produced by M. annularis.

Annual egg production by both Acropora palmata and A. cervicornis is 600 to 800 eggs per cm^2. The eggs are similar in size to those of Montastraea annularis in being about 300 pm in diameter.

Larvae and Juveniles

Little is known about the planula larvae of the four coral species treated here (Bak et al. 1977; Sammarco 1980; Rylaarsdam 1983). Settlement patterns are also poorly understood for any of the species reviewed here, but have been studied on reefs in Florida (Dustan 1977), St. Croix (Rogers et al. 1984), Netherlands Antilles (Bak and Engel 1979), and Jamaica (Rylaarsdam 1983). In all of these studies, coral recruitment was measured as the number of small corals (usually fewer than 4 or 5 cm in diameter) per unit area. These numbers cannot be translated into the numbers of larvae settled per square meter per year because it is not known what the early growth rates are, nor what patterns of settlement and mortality produce the observed counts of "juveniles."

In St. Croix (Rogers et al. 1984), juveniles of Acropora palmata occurred at densities of $0.1-0.3/m^2$ at depths of 3-9 m. Bak and Engel (1979) found similar densities ($0.13/m^2$) at similar depths.

Juveniles of Acropora cervicornis occurred at densities of $0.01-0.30/m^2$ at a depth of 9 m (Rogers et al. 1984). Bak and Engle (1979) found no juveniles of this species in surveys totaling 45 m^2 at appropriate depths. Rylaarsdam (1983), however, reported about $4.3/m^2$ on barren substrate 11 m deep chosen because settled larvae were abundant there.

Juveniles of Montastraea annularis live at densities of $0.09-1.04/m^2$ at depths of 9-27 m in St. Croix (Rogers et al. 1984), $0.20/m^2$ at depths of 3-9 m in Curacao (Bak and Engel 1979), and $2.33-9.32/m^2$ on bare substrates at a depth of 11 m in Jamaica (Rylaarsdam 1983).

Juveniles of Montastraea cavernosa are found at densities of $0.14-1.09/m^2$ at depths of 9-27 m and $0.05/m^2$ at 37 m on St. Croix (Rogers et al. 1984). In Curacao, densities are $0.07/m^2$ in 9-17 m and $0.20/m^2$ at 26-37 m (Bak and Engel 1979).

Although both species of Montastraea are common as adults on the Texas Flower Garden Banks, neither M. annularis nor M. cavernosa recruits to artificially -constructed settling plates there (Baggett and Bright 1985). The genus Acropora does not occur in either adult or juvenile form in this locality.

Phototransects on the north coast of Jamaica (Porter et al. 1981) revealed no conspicuous sexual recruitment of larvae in waters less than 20 m deep in 1976 or 1980 for any of the four species treated here. The difference between our study in Jamaica and the others mentioned above is that the phototransect method identified only corals that had successfully settled and grown into the light, where they could be recorded by the camera; in contrast, studies by Bak and Engel (1979), Rogers et al. (1984), and Rylaarsdam (1983) also included individuals that settled cryptically. These authors commented on (1) the disproportionate rarity of juveniles relative to the commonness of adults of these four species, and (2) the rarity of juveniles of these four species in relation to the commonness of juveniles in other taxa of corals, such as the lettuce corals (Agaricia).

The phototransect data from Jamaica (Porter et al. 1981) revealed that, by far, most recruitment of new coral colonies in all four species occurred by asexual rather than sexual reproduction. In both species of Acropora, fragmentation of adult colonies is the most common means of forming new colonies (Gilmore and Hall 1976; Davis 1977; Tunnicliffe 1981; Bak and Criens 1982; Neigel and Avise 1983). Fragmentation occurs during storms (Highsmith et al. 1980; Porter et al. 1981; Tunicliffe 1981; Highsmith 1982), but the susceptibility of a branch to breakage may be enhanced by boring by clionid sponges or lithophagan bivalves (Goreau and Hartman 1963; Neumann 1966; MacGeachy 1975; Hudson 1977). New colonies appear asexually in Montastraea by processes of fission or separation resulting from the death of intervening tissue.

GROWTH CHARACTERISTICS

Coral growth has been described in terms of either linear extension rates or rates of deposition of calcium carbonate (Bak 1973; Barnes and Taylor 1973; Dodge and Thomson 1974; Dodge et al. 1974; Buddemeir and Kinzie 1976; Gladfelter and Monahan 1977). Both linear extension and skeletal weight are known to be influenced by light (and its interaction with water depth and water clarity) and by sea temperature. What is known of the shallow water (<10 m) linear growth rates of the four species of interest is reviewed here.

Acropora cervicornis may be the most rapidly growing coral in the world in terms of linear extension (Chalker 1977; Chalker and Taylor 1978; Gladfelter et al. 1978). Linear extension rates were as great as 26.4 cm/year in Jamaica (Lewis et al. 1968), averaged 14.4 cm/year in Barbados (Lewis et al. 1968), and averaged between 5.1 cm/year (Vaughan 1915) and 10.0 cm/year (Shinn 1966) in Florida. Extension rates between 5.9-10.0 cm/year were measured in St. Croix, U.S. Virgin Islands (Gladfelter et al. 1978; Gladfelter 1984). All of these authors, together with J.W. Porter (unpublished data from Panama) recognized the extreme variability in growth rates from branch to branch on the same colony and from season to season on the same branch.

The growth rate and many other physiological parameters of Acropora cervicornis are adversely affected by increases in turbidity and sedimentation (Kendall et al. 1985). Acropora palmata grows at rates of 4.7-10.2 cm/year in St. Croix (Gladfelter and Monahan 1977; Gladfelter et al. 1978), 6-10 cm/year in Curacao (Bak 1976), and 5.0-9.5 cm/year in Florida (Vaughan 1915).

Literature on the growth rate of Montastraea annularis is extensive. Of special interest is the use of growth rates of this species in the Florida Keys as an environmental indicator of cold-water stress (Hudson et al. 1976; Hudson 1981, 1982) and water quality (Dodge et al. 1974).

Growth rates (cm/year) of Montastraea annularis were reported to be 0.81-0.90 in the Florida Keys (Agassiz 1890), 0.46 at Key West, Florida (Weber and White 1977), 0.68 (Vaughan 1915) and 0.50 (Macintyre and Smith 1974) in the Dry Tortugas, 1.07 in the Florida reef tract (Hoffmeister and Multer 1964), and 1.0-1.2 in Florida (Hudson et al. 1976). Elsewhere in the Caribbean, rates varied: 0.47-0.67 in Jamaica (Weber and White 1977; Dustan 1975), 0.66-0.89 in St. Croix (Gladfelter et al. 1978), 0.01-2.40 in Barbados (Lewis et al. 1968; MacGeachy 1975; Tomascik and Sander 1985), 0.68-0.73 in Curacao (Bak 1976), 0.50 in Panama (Weber and White 1977), and 0.71 in Belize (Weber and White 1977).

Growth rate decreases significantly as water turbidity increases (Dodge et al. 1974; Loya 1976; Dodge and Vaisnys 1977; Bak 1978). In water 2 m deep with low sediment resuspension rates of 0.5 mg x cm^{-2} x d^{-1}, maximum growth rates of M. annularis exceeded 1.1 cm/year and averaged 0.88 cm/year (Dodge et al. 1974); in areas of similar depth, but with higher sediment resuspension rates of 1.1 mg x cm^{-2} x d^{-1}, maximum growth rates were significantly lower and did not exceed 0.7 cm/year (average, 0.6 cm/year).

Linear growth rates of Montastraea cavernosa were 0.35-0.57 cm/year in the Dry Tortugas, Florida (Vaughan 1915), and 0.32 in Key West, Florida (Weber and White 1977). Average rates of 0.32 in Belize, 0.35 in Jamaica, and 0.32 in Panama were measured by Weber and White (1977).

POPULATION CHARACTERISTICS

Depth Distribution

As shown in part by the depth ranges and zones of maximum abundance of the four species treated here (Table 1 as determined in Jamaica), the basic zonation of almost all Caribbean coral reefs consists of Acropora palmata in shallow water, a mixed zone of A. cervicornis and Montastraea annularis just below this, and a zone, below 30 m, not always developed, where Acropora is absent and M. annularis and M. cavernosa dominate the horizontal surfaces. Species in the genus Agaricia dominate steeply sloping or vertical surfaces at these greater depths.

Response to Hurricanes

Hurricanes frequently influence reef structure. Moderate storms can be expected in southern Florida at least once every 5 years and severe storms perhaps once per decade (Jaap 1984). During the 20-year period 1966-85, however, the occurrence of severe storms in this region was unusually low. After Hurricane Allen (1980), Porter et al. (1981) demonstrated that in water less than 10 m deep, mortality was 95% in Acropora palmata and 98% in A. cervicornis, but only 15% in Montastraea annularis. (M. cavernosa was not common enouah in shallow water to enable quantification of its response to this storm.) At 30 m there was no damage to *A. cervicornis*, *M. annularis*, or *M. cavernosa*. (*Acropora palmata* was not found at this depth.) After the storm, mortality was 98% in fragments of *A. palmata* (J.W. Porter, unpubl. data) as well as in storm-generated fragments of *A. cervicornis* (Knowlton et al. 1981)--mostly due to intense predation from grazing snails (*Coralliophila*) and sea urchins, whose populations were little affected by the storm.

Morphologically, both species of *Montastraea*, but neither species of *Acropora*, are well equipped to survive moderate storms. However, the thick fronds of *A. palmata* and its interlocking branching morphology confers some degree of protection that *A. cervicornis* does not have (Ball et al. 1967; Stoddart 1969, 1974; Tunnicliffe 1981; Rogers et al. 1982). Further, *A. palmata* resists fracture better than *A. cervicornis* because of its continuous multiple bundles of axial corallites in its branch core (Constanz 1984). This may in part explain its distribution in more exposed areas.

From an evolutionary standpoint, it is probably not coincidental that most Caribbean coral species (including all of those reviewed here) reproduce during hurricane season when there would be a higher availability of newly bared substrate for successful larval settlement.

FISHERY

Commercial coral collecting has been banned in State of Florida waters since 1974 (Shinn 1979; Jaap 1984). Extension of this ban to all of the Gulf of Mexico and the South Atlantic has been recommended on the grounds that low growth rates and low yields make coral collecting similar to mining a nonrenewable resource (Anonymous 1982).

Poaching is almost impossible to prove, although it is probably common. Florida shell shops sell specimens of *Acropora palmata* and *A. cervicornis* at a high price. While these shops state that the specimens for sale come from Haiti, the high rate of sale of these spectacular branching colonies, and their ease of collection in Florida, may actually increase poaching on local coral populations.

Although Ross (1984) proposed a classical fisheries model to estimate maximum sustainable yield for a branching Pacific coral, his model did not incorporate partial mortality and fragmentation of colonies; consequently, further refinement will be required before it is applicable to Caribbean *Acropora*.

ECOLOGICAL ROLE

Photosynthetic Capability

Reef-building corals harbor the symbiotic dinoflagellate alga *Symbiodinium microadriaticum* (Taylor 1973; Trench 1979). New evidence (Blank and Trench 1985a, b) suggests that previously identified strains of this alga (Schoenberg and Trench 1980) may prove to be separate species. The alga constitutes only 5% to 15% of the dry weight of living tissue (Muscatine and Porter 1977), but the effect on the colony is profound; it causes coral heads of all of these species to produce more oxygen and fix more carbon than they consume, under optimal sunlight conditions (Table 2). For the last half century, a controversy has raged about whether corals get their food primarily from photosynthesis or by suspension feeding on plankton. That is to say, although they are taxonomically animals, are they functionally plants? *Acropora* corals look like plants and were so classified until the early 1800's.

Table 2. Patterns of primary production (maximum gross production (P) and nocturnal respiration (R) as $\mu g O_2\ cm^{-2} h^{-1}$) and instantaneous production/respiration ratios (P/R) for four reef-building corals (J.W. Porter, unpubl. data).

	Acropora palmata			Acropora cervicornis			Montastraea annularis			Montastraea cavernosa		
Depth (m)	P	R	P/R	P	R	P/R	P	R	P/R	P	R	P/R
1	89.5	14.3	6.3	34.4	7.7	4.5	109.9	30.6	3.6	62.2	26.2	2.4
10	52.9	11.8	4.5	42.6	8.2	5.2	56.9	20.6	2.8	42.6	21.3	2.0
30				37.4	6.8	5.5	55.8	16.0	3.5	43.8	14.6	3.0
50							44.7	14.0	3.2	26.9	11.6	2.3

Using polarographic oxygen chambers at various depths, Porter (1980) demonstrated that even at a depth of 50 m, Montastraea annularis was capable of effecting integrated 24-h production/respiration ratios (P/R) in excess of 1.0 (indicating autotrophy, or self-sufficiency, with respect to carbon) on sunny days. Autotrophy in the animal depends on the amount of fixed carbon that is transferred to the animal relative to the respiration of the animal. (See Porter et al. 1987 for an extensive review of the literature on photosynthesis and respiratory metabolism of this species.) However, if one integrates natural surface irradiance, including the seasonal effects of sun angle and cloudiness, colonies of M. annularis in water shallower than 10 m deep are capable of such autotrophy on a sustained basis; colonies of this species below that depth are not (Porter 1985). Colonies of M. annularis below 10 m must feed on particulate organic carbon (Lewis and Price 1975) or zooplankton (Porter 1974) to make up the deficit. At 50 m, the annual deficit is roughly 30% of the metabolic requirement (Porter 1985).

In examination of production rates, respiration rates, and instantaneous P/R ratios for the four species of corals under examination here, Table 2 reveals several trends. For all species, both production and respiration rates decrease with increasing depth (Davies 1977, 1980; Porter et al. 1987). Furthermore, at any given depth, the P/R ratios of branching Acropora are always greater than the same ratios for the mound-shaped corals Montastraea. This higher P/R ratio is reached because the Acropora species here have a combination of higher production rates (Chalker and Taylor 1978) and consistently lower respiration rates than the Montastraea species (Table 2).

As of 1986, the developing evidence suggests that, although the symbiotic association is an obligate one for these and other coral species, corals exist on a nutritional cline. The cline ranges from those like the Acropora, which are almost totally dependent on sunlight for survival, to those like Montastraea, which are less dependent on sunlight and more dependent on zooplankton for nourishment (Porter 1976; Lewis 1977). In this context it is useful to note that A. palmata drops out of the reef at the depth where its 24-h P/R ratio falls below 1.0 (J.W. Porter, unpubl. data). Mouth sizes and tentacle lengths also correlate with morphological (surface/volume) and physiological (P/R) ratios (Porter 1976). Polyps of M. cavernosa (Richardson et al. 1979) feed on zooplankton much more effectively than do 'polyps of A. cervicornis (Porter 1974).

The management implications of these basic biological data are clear: the branching Acropora species are much more susceptible to increases in water turbidity than are the mound-shaped Montastraea (Dallmeyer et al. 1982). Dredging or pollution that reduces the long-term water clarity can reduce P/R ratios below unity for all four species. Species of Acropora may not be able to compensate with an alternate food supply, such as zooplankton, which is used by Montastraea colonies. One expected result is that the depth distribution of Acropora will be truncated in turbid water (Griffin 1974; Johannes 1975; Loya 1976; Dodge and Vaisnys 1977; Bak 1978; Kendall et al. 1985). Under conditions of turbidity, Loya (1976) noted a reduction in the densities of colonies of Montastraea annularis and an increase in the densities of colonies of M. cavernosa.

Interspecific Competition

Lang (1973) described the ability of reef corals to extend their mesenterial digestive filaments onto a neighboring coral species and digest away its living tissue. A dominance hierarchy exists within the coral species. The defense hierarchy for the four species examined here is Montastraea annularis > M. cavernosa > Acropora palmata > . cervicornis (Lang 1973). Species-in the family Acroporidae are generally at the bottom of the pecking order, whereas species in the family Faviidae are generally near the top. Lang (1973) has speculated that the superior defense abilities exhibited by favid corals like Montastraea may be a compensatory mechanism for the superior overgrowth capabilities of the acroporid species. These allelochemical mechanisms may be of special significance in periods between hurricanes, because catastrophic storms always favor the massive morphology of Montastraea over the branching morphology of Acropora.

Although the attack patterns of extracoelenteric destruction were initially thought to be a fixed property of each species (Lang 1973), P. Dustan (Department of Biology, College of Charleston, Charleston, S.C., unpubl. observations) identified several forms of M. annularis which destroy each other. In addition, the pecking order for the 65 species of hermatypic coral species in the Caribbean is not identical for all localities (Lang 1973).

Predators

All four species reviewed here are subject to predation, but "plagues" of coral predators such as Indo-Pacific Acanthaster (the crown-of-thorns starfish) observed by Endean (1976) have not been described for the Caribbean.

A major coral predator is the polychaete bristle worm Hermodice carunculata (Glynn 1962; Marsden 1962; Ebbs 1966; Lizama and Blanquet 1975; Antonius 1977). This predator impales itself on the long branches of A. cervicornis and denudes the branch tips of their living tissue. The predation marks show up as scars several centimeters long on A. cervicornis. Hermodice also digests tissue of A. palmata and both Montastraea species; on these forms the predation scars appear as white patches.

The coral-shell gastropod Coralliophila abbreviata is also a major predator on all four species of corals treated here (Rylaarsdam 1983; C. Rosesmyth, Department of Zoology, University of the West Indies, Kingston, Jamaica; unpubl. data). Its preferred food is Acropora cervicornis, but it also feeds extensively on Montastraea annularis. After Hurricane Allen, when Acropora populations were decimated by storm damage, C. abbreviata significantly reduced the Acropora populations further. Populations of Acropora that were healthy before the storm could sustain a low level of snail predation. This same predation level after the storm decimated the few remaining Acropora colonies (Knowlton et al. 1981).

Although not widely documented, the long-spined sea urchin Diadema antillarum is known to eat Acropora (Bak and Van Eys 1975; Sammarco 1980, 1985). It does so actively when starved, but may also do so adventitiously while feeding on turf algae growing next to coral tissue.

Hermit crabs such as Petrochirus diogenes and Paguristes sp. live between the branches of both species of Acropora (Gilchrist 1985). They sometimes cause extensive damage, and can decimate their host species locally when their population numbers are high.

Finally, the three-spot damselfish Pomacentrus planifrons Cuvier establishes algal gardens on branching Acropora when it is available and on Montastraea annularis when Acropora is rare (Thresher 1976; Brawley and Adey 1977; Kaufman 1977; Itzkowitz 1978; Williams 1978; Sammarco and Carleton 1982). The fish nips off the living coral tissue and weeds the garden as algae begin to grow on the bared coral skeleton.

Predation of any kind may be repaired by tissue regeneration over the dead region, or the area may be colonized by other epibiota. These dead regions may allow settlement by boring sponges and bivalves that can further weaken the skeleton (MacGeachy 1975; Bak et al. 1977)

Sediment Rejection Behavior

Sediment rejection is an important behavioral characteristic influencing the growth, survival, and distribution of reef corals. The four species considered have differing abilities to shed sediment. Hubbard (1973) and Hubbard and Pocock (1972) ranked them in terms of their ability to remove silt (particles <62 µm in diameter), fine sediments (62-250 µm), and coarse sediments (250-2,000 pm). Acropora palmata and A. cervicornis were unable to remove coarse sediments and only weakly able to remove fine sediments. Montastraea annularis and M. cavernosa, on the other hand, were weakly able to remove coarse sediments and highly competent at removing fine sediments. In all four species, ciliary movements remove silt and clay-sized particles. Hubbard and Pocock (1972) showed general correlations between coral zonation and sediment-rejection capability.

Although it is clearly an influencing factor, the differential response to hurricanes, ordinary storms, light gradients, turbidity, other physical effects, and biotic interactions are probably of greater causal importance than sediment rejection properties in determining the overall vertical and lateral distribution of these species along a reef. Further, the effect of suspended sediments, even when successfully shed, tends to increase respiration and decrease photosynthesis (J.W. Porter, unpubl. data). Photosynthesis decreases because of reduced light penetration, and P/R ratio is concomitantly reduced (Dallmeyer et al. 1982). Water movement (turbulence) and gravity are probably more important in removing sediments from the branching Acropora species than are their capabilities for sloughing sediments in stagnant water.

Disease

Coral diseases are not well understood (Voss 1973; Antonius 1982; Bak 1983; Peters 1984). Two diseases recently received considerable attention in the Florida area. The first is "white-band" disease, occurring in epidemic proportions on Floridian colonies of Acropora palmata (Jaap 1984). Gladfelter (1982) demonstrated that this unidentified pathogen also severely reduced populations of A. palmata in St. Croix, U.S. Virgin Islands. This disease also attacks A. cervicornis (J.W. Porter, unpubl. data).

The second disease is caused by infections of the blue-green alga Phormidium corallyticum (Antonius 1977, 1982; Rutzler and Santavy 1983; Taylor 1983; Rutzler et al. 1983). Because of its appearance as a black ring around the infected area, it has been called the "black-band" disease. It kills both species of Montastraea, but neither species of Acropora (Rutzler et al. 1983). It may be the same disease described by Mitchell and Chet (1975) and Ducklow and Mitchell (1979a, b) as an unidentified bacterial infection.

Cancerlike ulcers have also been described on corals (Preston 1950; Squires 1965; Bak 1983; Peters 1984; Peters et al. 1986).

In all cases of algal or bacterial disease, prior stress to the coral increases both the likelihood that an individual colony will contract a disease and the likelihood that it will subsequently be killed by it (Peters et al. 1986).

ENVIRONMENTAL REQUIREMENTS

In general, the environmental requirements of all reef-building corals are narrow. Clear, warm, well-oxygenated sea waters of constant salinity, such as that off southern Florida (Churgin and Halminski 1974a, b; NOAA 1981) are requisite for the development of coral reefs. I describe here some of the minor differences between the four present species.

Temperature

Acropora cervicornis and A. palmata are highly sensitive to lower than usual temperatures (Mayer 1914, 1916; Shinn 1976; Porter et al. 1982). In January 1977 surface waters on the Dry Tortugas reefs dropped to 14 °C (Walker 1981). About 96% of all Acropora colonies in water less than 2 m deep, died during this cold-water intrusion; Montastraea was too rare at this depth to allow measurement of mortality (Porter et al. 1982). At 13 m, where water temperatures may not have been as low, mortality was 15% in Acropora but only 2% in Montastraea. In Bermuda, surface water temperatures as low as 8 °C have been recorded (Verrill 1902); no species of the genus Acropora live off Bermuda. Low water temperature probably limits the northward extension of Acropora in Florida. Perhaps Montastraea is found much farther north than Acropora on both the gulf and Atlantic coasts of Florida (Figure 2) because it is capable of flourishing in deeper water with less temperature stress.

Cold stress can also affect Montastraea, which has a lower lethal temperature of 13.9 °C (Mayer 1914, 1916). Cold- or warm-water stresses occur frequently at Hens and Chickens Reef off Plantation Key, because these reefs lie near Florida Bay, where temperature fluctuates greatly in response to atmospheric conditions (Lee and Mooers 1977). Cold stress has been well documented in M. annularis as distinct skeletal bands of high density, or whole or partial mortality of colonies (Hudson et al. 1976; Dustan 1977).

Although August temperatures average 29.3 °C in the Dry Tortugas and

28.7 °C at Fowey Rocks (Vaughan 1918), water temperatures as high as 31 °C have been recorded (Vaughan 1918). Mayer (1918) reported that the upper lethal temperature is 35.8 °C for A. palmata, and 33.8 °C for A. cervicornis (Shinn 1966). These elevated temperatures would occur only in coral habitat at the surface and under unusual oceanographic conditions (Jaap 1984). Jaap (1979) recorded an example of putative heat stress at Middle Sambo Reef, Florida, involving bleaching and loss of symbiotic zooxanthellae from A. palmata and A. cervicornis. Affected specimens recovered after 6 weeks.

Salinity

Corals prefer salinities between 27 and 40 ppt (Lewis et al. 1968). Both Acropora and Montastraea can survive 1-h exposure to seawater approaching 20 ppt, such as occurred after torrential rains in Panama in 1971 (J.W. Porter, unpubl. data), but coral reefs never occur where oceanic salinities are consistently below 33 ppt. Typical responses to lowered salinity are the loss of zooxanthellae (Goreau 1964) and the production of mucus (Coffroth 1985). It is unclear whether the absence of corals in slightly brackish water is due to the reduced salinity itself, to increases in suspended sediments, or temperature fluctuations often associated with areas of inflowing freshwater (Dole and Chambers 1918).

Dissolved Oxygen

Like all coral species, the four species reviewed here exist where dissolved oxygen rarely extends beyond the range of 90% to 125% saturation (Jaap and Wheaton 1975). Montastraea annularis tolerates oxygen tension above 100% (Wells and Wells 1971), and probably most coral species are able to tolerate very high oxygen tensions because the coral tissue contains algae that produce large amounts of oxygen. As a correlate of this, corals contain high concentrations of superoxide dismutase, a compound which burns off excess oxygen (Dykens and Shick 1982). Conversely, given the ability to produce oxygen, corals are also able to tolerate waters with exceedingly low oxygen tensions (Burris et al. 1983). In closed respirometry experiments in which the flush-pump failed but where the oxygen recorder continued to work (J.W. Porter, unpubl. data), both Acrdpora cervicornis and M. annularis tolerated oxygen tensions as low as 1.0 ppm for 1 h, but both died when these-conditions persisted for 6 h.

The absence of these species in seawater in which oxygen is less than saturated, like their absence in water of low salinity, probably reflects intolerance to both depressed oxygen levels and associated factors rather than to low dissolved oxygen alone.

Substrate

All four of these corals must settle and grow on a stabilized, shallow (Table 1) sea floor. Neither the adults nor the attached juveniles are capable of surviving in areas of heavy sedimentation (Hubbard and Pocock 1972). All four species can colonize stable vertical or sloping substrates above sandy bottoms, and large detached fragments of Acropora cervicornis can roll into sandy areas and colonize them (Tunnicliffe 1981), and thus support the development and spread of patch reefs.

Solar Irradiance

Light intensity decreases rapidly with increasing depth (Gordon and Dera 1969; Brakel 1979; Dustan 1982). As judged by work in Jamaica on Acropora (Porter 1980) and Montastraea (Porter et al. 1987), A. palmata is most abundant where the maximum ambient irradiance reaches 1,200-1,800 µE $m^{-2}s^{-1}$ and optimal integrated daily irradiance is about 28 E $m^{-2}d^{-1}$.

Populations of *A. cervicornis* flourish where peak ambient irradiance levels are 300-800 $\mu E\ m^{-2}s^{-1}$ and optimal integrated irradiance approaches 15 $E\ m^{-2}d^{-1}$. *Montastraea annularis* populations dominate substrates over a broader depth range but still are most common where maximum instantaneous light intensities are 200-800 $\mu E\ m^{-2}s^{-1}$ and integrated values approach 10-15 $E\ m^{-2}d^{-1}$. *Montastraea cavernosa* is most common just below the zone of greatest development of *M. annularis*. Here peak light intensity reaches 600 $\mu E\ m^{-2}d^{-1}$ and the integrated daily total approaches 12 $E\ m^{-2}d^{-1}$. Both *M. annularis* and *M. cavernosa* are still-common at 65 m, where instantaneous light does not exceed 50 $\mu E\ m^{-2}s^{-1}$ and daily totals do not exceed 2 $E\ m^{-2}d^{-1}$.

Solar radiation probably controls the intensity and timing of reproductive activity in all four species. This may be especially true for *M. annularis* and *M. cavernosa* because most of their -colonies exist well below their light compensation depth, where their integrated production/ respiration ratio is below 1.0 (Porter et al. 1987).

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16. Abstract (Limit: 200 words)

Species profiles are literature summaries of the taxonomy, morphology, range, life history, and environmental requirements of coastal aquatic species. They are designed to assist in environmental impact assessment. Four species of reef-building corals are considered: elkhorn coral, staghorn coral, common star coral, and large star coral. All four species spawn annually in the fall during hurricane season. Juvenile recruitment is low in all four species. Rapid growth rates of species in the genus Acropora (10-20 cm/yr) contrast with slower growth rates of species in the genus Montastraea (1.0-2.0 cm/yr), but both species of Montastraea are also important in reef development due to their massive form and great longevity. Shallow-water colonies of Montastraea survive hurricanes; shallow colonies of Acropora do not. Because of their dependence on photosynthesis for all of their carbon acquisition, the Acropora species reviewed here have a more restricted depth distribution (0-30 m) than do the Montastraea species considered (0-70 m). All four species are subject to intense predation by the snail predator, Coralliophila. Species of Montastraea are susceptible to infection from blue-green algae, which produce "black band disease"; species of Acropora are susceptible to a different, as yet unidentified pathogen, that produces "white-band" disease. Increased water turbidity and sedimentation cause reduced growth rates and partial or whole mortality in all four species.

17. Document Analysis a. Descriptors

Growth	Salinity	Reefs	Feeding habits
Photosynthesis	Temperature	Coral	Sediments
Life cycles	Depth	Oxygen	

b. Identifiers/Open-Ended Terms

Reef-building corals	Elkhorn coral	Acropora palmata
Staghorn coral	Acropora cervicornis	Montastraea annularis
Large star coral	Montastarea cavernosa	Common star coral

c. COSATI Field/Group

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